

TAXONOMY AND ZOOGEOGRAPHIC RELATIONSHIPS OF THE
SOUTH AMERICAN NAIADES (PELECYPODA: UNIONACEA AND MUTELACEA)¹

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ABSTRACT

A natural system of classification is proposed for the South American fresh-water pearly mussels which were formerly all grouped in the superfamily Unionacea. The systems recognized since the end of the last century which were based mainly on conchological, and partly on anatomical characters, are here discussed in relation to recent embryological and phylogenetic research, especially as regards the structure and development of the different types of larvae. Researches made by the authors during the last decade have confirmed the existence of the "lasidium" larva, discovered by Ihering in 1891, but not observed since by other authors. This larva is typical of the South American genera *Anodontites*, *Mycetopoda*, *Monocondylaea* and *Leila*. At the same time the research of other workers on African species of *Mutela* has revealed the existence of a larva which, if not entirely similar to the lasidium, is similar in its basic structural features. Comparative studies of such structures and their development show a family differentiation between Mutelidae of Africa and Mycetopodidae in South America. On the other hand, the close relation between these two families, and their extraordinary embryological divergence from those other fresh-water mussels characterized by the well known "glochidium" larva, warrants the distinction of a new superfamily, MUTELACEA. All other South American fresh-water mussels with larvae of the glochidium type remain in UNIONACEA.

The Mutelacea are living today in the southern hemisphere, excepting Australasia, whether South American groups are derived from African groups, or vice versa, is not known. The anatomical and embryological differences between Mutelidae and the more advanced Mycetopodidae seem to indicate an ancient separation. Paleontological records are rare: none exist for Africa or Australasia; in North America, fossil casts from the Triassic of Pennsylvania were referred to by Pilsbry as a *Mycetopoda*-like mussel; *Pleiodon priscus* described by Ihering from the Cretaceous of Brasil is not a mutelid, as was assumed, but belongs to the genus *Paxyodon* (Hyriidae). Some references to *Anodontites*-like fossils from the Cretaceous of Bahia, Brasil are very doubtful.

The South American Mutelacea, i.e., the Mycetopodidae, are divided into 3 subfamilies: Mycetopodinae, Anodontitinae and Monocondylaeinae; another subfamily, Leiliinae, might be accepted in view of more recent anatomical and embryological research. Other groups, at the subfamily level, indicated in previous classifications, cannot be maintained, their characters being insufficient and the intergradations numerous.

The South American Unionacea belong to the family Hyriidae, which also occurs in Australia but is absent in the rest of the world; the exclusively South American forms belong in the subfamily Hyriinae and are divided into 3 tribes: Diplodontini, Castaliini and Prisdontini. Especially the Diplodontini, largely formed by the genus *Diplodon*, are more closely related to forms of Australia and New Zealand. Here again, attempts to separate a number of subgenera have failed on account of the difficulty of defining constancy of characters. From the embryological point of view, however, we may distinguish two entities of subgeneric value: *Diplodon s.s.*, with parasitic glochidia, and *Rhipidodonta* with non-parasitic glochidia, i.e., having direct development. There is paleontological evidence of Hyriidae in the North American Triassic, the Paleocene of Southern Argentina, and the Eocene of Chile, the latter fossils being very similar to the species now living in the region as well as to related groups from Australia. All these fossils belong to the genus *Diplodon*, of which other species are known from the strata, at different levels of the middle and upper Tertiary, scattered over the continent of South America.

The monotypic genus *Bartlettia* of the so called "fresh-water oysters", currently included within the Etheriidae, very probably belongs to a polymorph species of Mutelacea, *Anodontites tenebricosus*. Larval stages of Etheriidae are unknown, but further investigation may prove that the family, if it should be maintained as such, integrates with the Mutelacea.

Comparative tables are given of the different systems of classification since 1900 as well as of the new system adopted here, from the superfamily down to subgeneric level.

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The current system of classification of the Neotropical fresh-water mussels dates from the end of the last century, with important improvements made during the last three or four decades (Table 3). Some anatomical characteristics favor the concept of a single family, Mutelidae, with many genera not only from South America, but also from Central America, Africa and Australasia. The anatomical similarities, however, are not consistently present, and embryological and conchological characters, as well as zoogeographical factors, are at variance with that concept of singleness. From the biological point of view, especially, the division of Mutelidae into Mutelinae and Hyriinae is fundamentally more distinctive than a separation at merely the subfamily level.

In 1891 Ihering described a larval form, from one species of Mutelinae, *Anodontites wymanni* Lea (= *A. patagonica* Lamarck) which was entirely different from the "glochidium" larva until then considered common to all Unionacea. That type of larva, named "lasidium", has a body divided into three recognizable regions: the anterior, ciliated and somewhat conic or bell-shaped; the median, rounded and covered by an indivisible shell, and the posterior, forming two short lobes with cirri or hooks placed in rows. Two peculiar ribbon-shaped appendages of considerable length evolve from the anterior end. Ihering later added the following remarks to the description: "I know this larva only in *Glabaris* [= *Anodontites*], but in *Aplodon* [= *Monocondylaea*], the anatomy and the egg agree so well that the larva can scarcely differ. It is advisable now, to follow further the distribution of this larva in America and Africa" (Ihering 1893: 59).

Because of the remarkable differences between the two types of larvae and the fact that subsequent investigators failed to find, or to recognize, the lasidium, the existence of this larva remained doubtful. Its rediscovery was reported by Bonetto (1951) with a preliminary description of the lasidium of *Anodontites trapesialis* from the Parana River, and further investigations revealed its presence also in

Monocondylaea and *Mycetopoda*. The organization and development of the lasidium proved to be more complicated than could be inferred from Ihering's original diagnosis. Franc (1949) said that he found "glochidia" (!) in the gills of *Mutela dubia* and *M. rostrata*, but more recently (1959 and 1961) Fryer of the East Africa Fisheries Research Organization, in Uganda, gave a complete description of the larva of *Mutela bourguignati*, with important and detailed observations of its development. Its basic structure is that of a lasidium, although it is differentiated from the embryos of the South American genera by marked morphological features.

COMPARISON OF THE LARVAE OF THE AFRICAN AND SOUTH AMERICAN "MUTELIDS"

The African Larva

The embryo described by Fryer from *Mutela* (Fig. 1) has the anterior end of the body divided into two short lobes. The second portion is covered by a single univalve shell, furnished at the end with two rows of 3-7 small hooks and a row of small spinulae. It develops while attached externally to the body of a fish, probably by means of the hooks.

The larval shell is folded on the sides and fused at the median ventral line, forming an integral, not bivalved, piece (Fig. 2, LS). This shell is uncalcified.

As the larva grows, two tubular appendages, called "haustoria" by Fryer, are produced anteriorly, penetrating into the fish's tissues and, apparently, acting as both trophic and fixing organs. After this the organism experiences a complete metamorphosis conducive to the organization of the juvenile mussel, and finally the haustoria-base is cut, initiating the free living stage. The size of this larva is over 150 micra, almost twice as large as the lasidium known in the South American species. Larval specimens of *Mutela*, kindly sent by Fryer, in different stages of development, allowed a more complete comparative study.

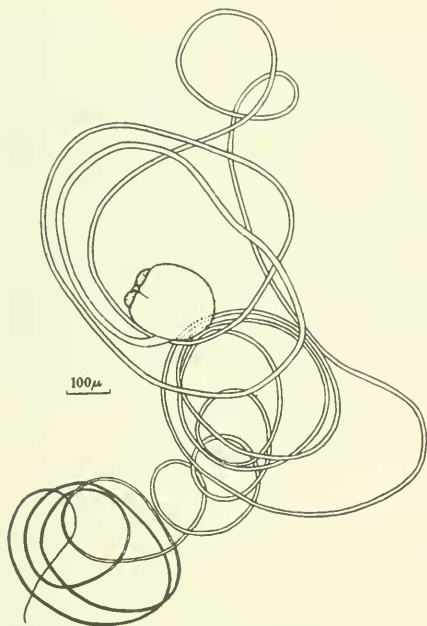


FIG. 1. Larva of *Mutela bourguignati* (Ancey) showing the long tentacle (from Fryer).

The South American Larva

Investigations on the lasidium of *Anodontites trapesialis forbesianus* (Lea) and its parasitic phase in fishes, revealed a coincidence of development with that of *Mutela*, but without formation of the tubular appendages or haustoria indicated by Fryer. The larva is attached to the host by a cyst-like structure.

The lasidium of *Anodontites* (Figs. 3-4) is smaller, measuring an average of 85 micra or 56.6% of the size of the larva in *Mutela*.

The two ciliated lobes of the frontal portion, already indicated by Ihering, have an elongate-conic shape, but it is observable that the frontal portion can be separated into two circular pieces, lying side by side, and projecting shortly from the embryonic shell. This section coincides, in general, with that of *Mutela*.

The filamentous appendages are very different. Ihering said that they consist of two wide flat ribbons emerging laterally,

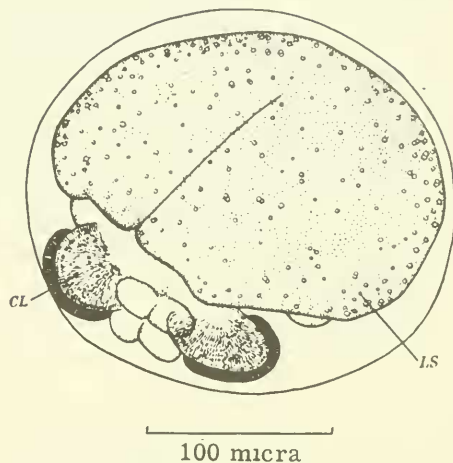


FIG. 2. Larva of *Mutela bourguignati* (Ancey), oblique-dorsal view (from Fryer 1961, Fig. 3). CL ciliated lobes; LS embryonic shell.

but in fact they seem to project from a more ventral position, in the portion half covered by the valve; they then expand, fused over the shell at the base of the anterior ciliated lobes. Thus, a conic enclosure is formed, with the apex toward the anterior lower side of the larva. The upper margins of the ribbons remain free, forming a V-shaped canal extending about ten times the length of the larval body, and then dividing into two or three branches. Although the complexity of this process establishes a remarkable difference with *Mutela*, the position of the axes are essentially similar.

These differences, however, are considerable reduced in *Monocondylaea*, in which the lateral expansions are less developed, and also in *Mycetopoda* whose filament has no lateral expansions at all, as in *Mutela*. In *Leila* the lasidium differs from that of *Anodontites* by its larger size the ribbon-like appendages are narrower, become thinner distally and the cirri or

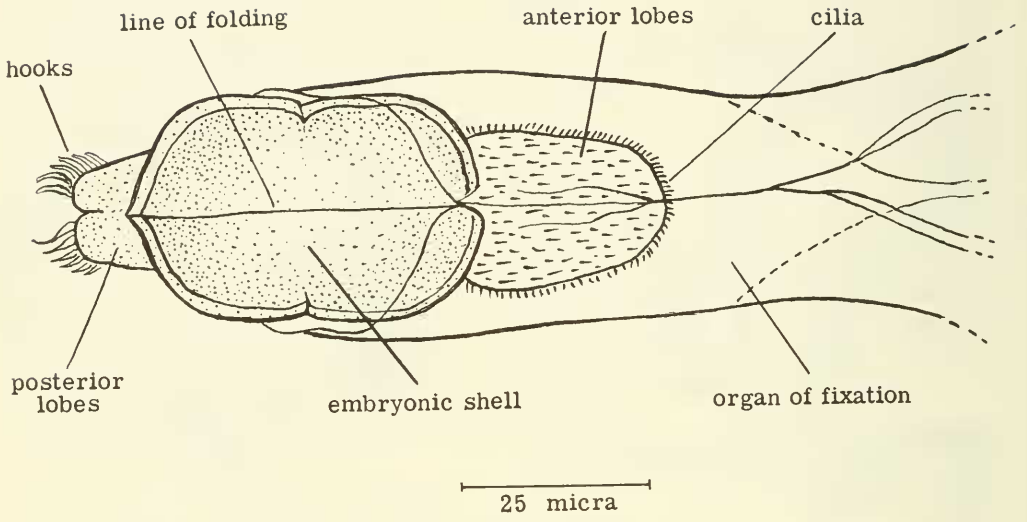


FIG. 3. Lasidium of *Anodontites trapezialis forbesianus* (Lea). Dorsal view.

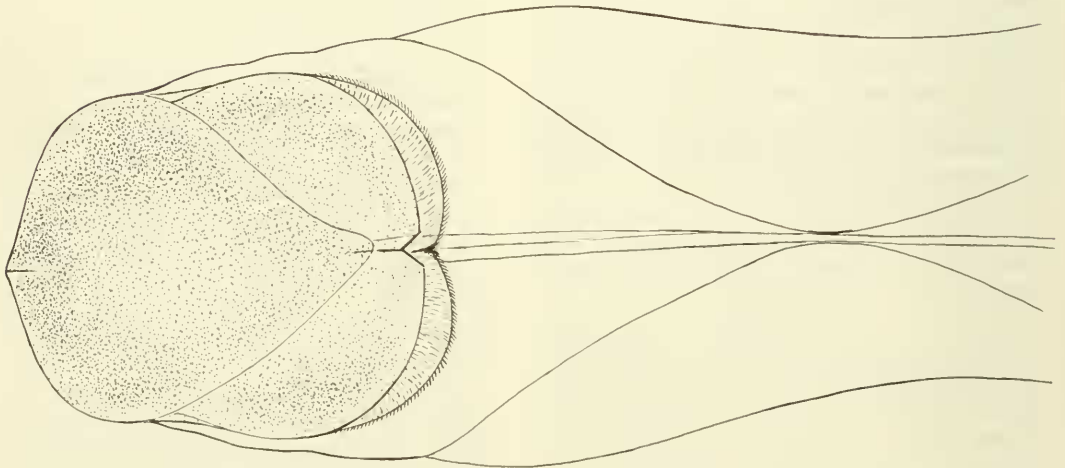


FIG. 4. Same as Fig. 3, with division of the anterior lobes, and posterior lobes not visible (folded ventrally).

hooks of the posterior end are apparently, wanting.

In the larval body, the outstanding characteristic in both African and South American forms is the uncalcified univalve shell (Fig. 5), whereby they differ essentially from the glochidia. The posterior end of the body is usually folded under the ventral side, and shows curved cirri or hooks (6 - 7 in *Anodontites trapezialis*) forming a circle around a pair of lobes; additional spinulae like those in *Mutela* are absent.

COMPARATIVE DEVELOPMENT OF THE JUVENILE MUSSEL

The larva, inside the single, non-bivalved enclosure follows divergent ways in *Mutela* and *Anodontites*.

In *Anodontites*, the extremities are folded toward the center of the ventral side, while in *Mutela* the growth is longitudinal. The period of development is 25 days in *Mutela*, but may be shorter or longer in *Anodontites*, 19 to 28 days. As a consequence of the differences in their parasitic adaptations, the young mussel in *Mutela* has an elongated body, regularly curved below and somewhat truncated anteriorly; in *Anodontites* it is short and high (Fig. 6) and the surface of the valves is formed by a series of planes, offering a polyhedral shape. In both cases the cuticle of the embryonic shell adheres to the valves of the juvenile mussel, and the small and cylindrical ligament is located on the middle of the hinge line, simulating a chondrophore. In the first stage the shell is composed only of conchiolin, but it is slowly filled in isolated spots with calcium carbonate.

The internal organization is similar in both *Mutela* and *Anodontites*. The foot has a rudimentary byssogenous gland with its separate channel, but some elements of fixation indicated by Fryer for *Mutela* are not found in *Anodontites*; also, in the foot of the latter, there is a pair of very large otocysts. Both adductors are present. The branchiae, formed by 13 ctenidia in *Mutela* and 7 - 8 in *Anodontites*, are in a

single row at each side; they develop from small papillae and are separated during the first days of life. The labial palps, digestive tract and heart do not differ. The mantle in *Anodontites* is closed from the beginning to form the siphons, which do not occur in *Mutela*.

The ontogenetic processes in the African and the South American forms are of evident common ancestral relationship. They probably separated from all other Naiades with glochidia at a very early time in their evolution. On the basis of their marked differences a more natural system of classification can be established.

TAXONOMIC CONSIDERATIONS (Compare with Table 3)

Without discussing the very early essays of classification that were merely conchological, and artificial in their results, it is necessary to return to Simpson's synopsis of 1896, for the first seriously founded system.

Simpson distinguished two large families, Unionidae and Mutelidae, the first with schizodont hinge and glochidium larva, and the second with taxodont hinge (theoretically) and lasidium larva, thus accepting Ihering's discovery, although it was yet unknown how many genera had this larva. The Unionidae included forms from all continents in different degrees of relationship, and Mutelidae confined to the Neotropical region and tropical Africa.

Since then, from the intensive and valuable work of Ortmann, to the most recent speculations on classification, such as those of Modell, several systems have been proposed, but they only complement or modify that of Simpson. Ortmann grouped the neotropical and notogeic forms of Unionidae (equivalent to the "Lamphorhamphus" group of Simpson), with the Mutelidae of Africa and South America, in a single family Mutelidae, based on anatomical details of certain relevance, and also because the marsupia for the incubation of the larvae were located in the inner laminae of the gills. He separated the Mutelidae into subfamilies Hyriinae

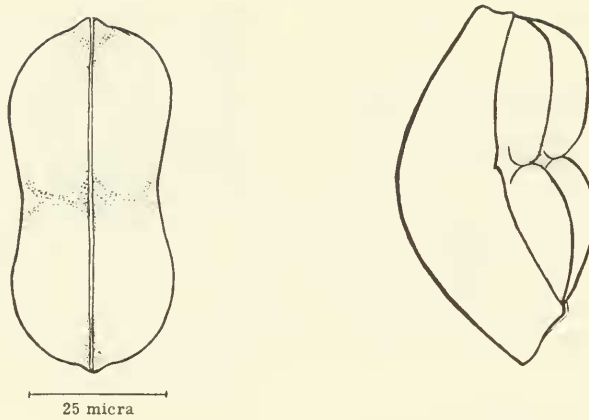


FIG. 5. Larval shell of *Anodontites trapeziales*, dorsal and lateral-ventral views, in the first day of parasitism on the fish *Jenyssia lineata*.

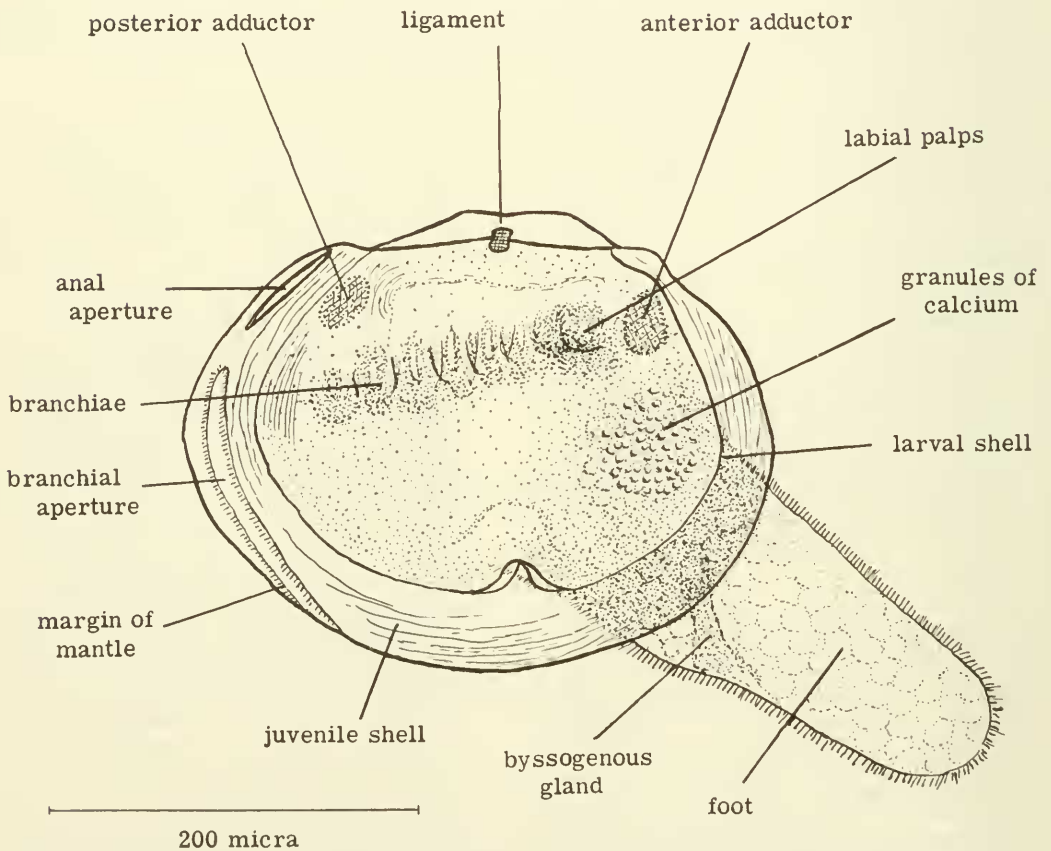


FIG. 6. Juvenile mussel of *Anodontites trapeziales* with new shell, and larval shell still attached.

and Mutelinae.

The differences between the African, South American and all other known Naiades are so remarkable that in all probability they do not belong to directly related groups, but rather represent divergent ways in the conquest of continental waters. The two different types of larvae, i.e., glochidium and lasidium, cannot be considered to be derived one from the other or from any hypothetical direct ancestry. Ortmann's sound and critical observations of the the anatomical and conchological characters, add support to such a conclusion. It is necessary to upgrade the taxonomic categories in the family group in order to adjust the system to our present knowledge.

The most important, and the most overlooked, of Ortmann's taxonomical considerations were his own reservations with regard to the stability of the system. He said in fact (1921: 454) that: "It possibly might be advisable, in future, to elevate the two South American subfamilies to the rank of families...", and "the *Mutelidae* of Simpson (1900) correspond to our *Mutelinae*" (p. 455 footnote). Pg. 567: "although closely allied to *Spatha* [= *Mutela*], the South American genera form a group by themselves, and the [only] similarity of *Mycetopoda* to *Spatha* in the anal opening apparently indicates only parallelism of development, no genetic relationship", and also (p. 568) that "According to our present knowledge, the two subfamilies are un-

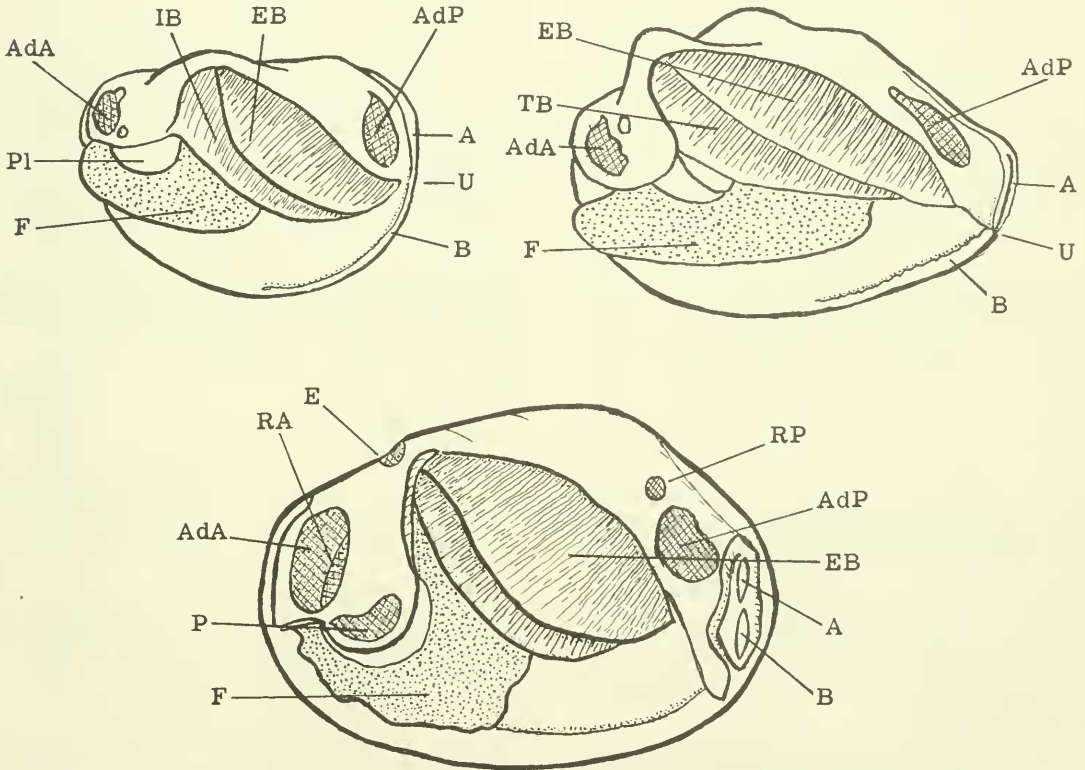


FIG. 7. Anatomy of South American and African naiad genera. Top, left: *Anodontites* (Mutelacea, Mycetopodidae); top right: *Castalina* (Unionacea, Hyriidae); below: *Spathopsis* (Mutelacea, Mutelidae). A, anal opening; AdA, Adductor anterior; AdP, adductor posterior; B, branchial opening; E, elevator or dorsal scar; F, foot; EB, external branchia; IB, internal branchia; Pl, palps; P, protractor; RA, retractor anterior; RP, retractor posterior; U, union of mantle separating anal and branchial openings.

doubtedly allied; but they are very sharply separated by anatomical as well as shell-characters, and it is impossible to form an appropriate idea of their genetic connection".

Regarding the condition of primitiveness in these groups, Ortmann remarks: "It is not very likely that the Mutelinae reached South America coming from Africa" (p. 455). "It is hard to say which group is more primitive, since of the two differing characters, the one (anal opening is more primitive in the American forms, the other (inner lamina of inner gill) more primitive in the African *Spatha*" (p. 567).

These observations would have been sufficient to justify the separation, even if the system was based only on anatomy and not on the embryology of the larger groups. Ortmann used the study of the South American larvae to diagnose species, sometimes genera, but not at the family level. So it is that both lasidia and glochidia are included in his Mutelidae, although the larvae from African species were then still unknown and the South American lasidia continued unobserved after Ihering.

The numerous genera developing through the embryonic stage of glochidium, are separated into several families, according to anatomical peculiarities, such as Margaritiferidae, Unionidae, and Hyriidae. Consequently, the larval condition has a taxonomic value, not merely at the family but at the superfamily level. We have seen that, in the current system, it has only a minor importance, generic or specific. We believe that adult mussels developing from totally different embryos should not be in the same superfamily.

In conclusion, the Superfamily UNIONACEA should be restricted to those groups with glochidium larva, and those with lasidium elevated to a new Superfamily MUTELACEA.

A synoptic comparison of the two families which comprise the MUTELACEA, i.e., Mycetopodidae and Mutelidae, is given in Table I.

THE SOUTH AMERICAN MUTELACEA

The family Mutelidae is only known from Africa. In the New World they are replaced by Mycetopodidae, characterized by a hinge that is edentulous or has very rudimentary teeth; by a wide prismatic layer on the internal margin of the valves, the presence of a supra-anal aperture, the connection of the inner laminae of the branchiae with the visceral sac, and the absence of dorsal muscle scars. The differences between the lasidium and the lasidium-like larva of Mutelidae already have been indicated.

In South America the two superfamilies Unionacea and Mutelacea, occupy overlapping areas, though there are but marginal zones, having only the one or the other; these zones perhaps correspond to different origins and times of dispersion. The Mutelacea (Mycetopodidae) are more restricted in their southward distribution (Map 1), occupying zones north, east and peripheral to the Pampas-Chaco districts, and some tributaries that cross these districts and empty into the Parana River. In the affluents of the left side of the Parana River the Mutelacea have a greater development than the Unionacea (Hyriidae) (Compare with Map 2). In the northwest they extend into Central America and Mexico, where the Hyriidae are absent.

Invasion of northern forms into the lower La Plata River system probably occurred in relatively recent times (the basin as it is known today, was formed during the Pleistocene), through connection of tributaries of the Upper Paraguay with those of the Amazon, as is the case with *Anodontites ensiformis*. Only a single species, *Anodontites puelchana* (d'Orb.) is rarely found in northern Patagonia. No species are known west of the Andes, in Peru or Chile, a zone which is populated by Hyriidae of the genus *Diplodon*.

TABLE 1. Comparative Characters of Mutelacea

	Mycetopodidae (Neotropical)	Mutelidae (African)
Larva:	<p>lasidium</p> <p>with spinulae</p> <p>parasites forming cysts</p>	<p>lasidium-like but with different development</p> <p>without spinulae</p> <p>parasites through tubular appendages</p>
Young mussel:	<p>with mantle closed</p> <p>with more than 70 ctenidia</p> <p>shell short</p>	<p>with mantle open</p> <p>with less than 20 ctenidia</p> <p>shell elongated</p>
Inner laminae of gills:	usually connected with abdominal sac	free
Dorsal scars:	absent except in <i>Leila</i>	single and well developed
Anal opening:	not closed above, except in <i>Mycetopoda</i>	closed above, not forming supra-anal opening
Hinge:	toothless or single toothed, never taxodont	taxodont when present
Umbonal sculpture:	absent or with concentric waves	when present, rugose resembling some unionid types
Distribution:	South America except West side of the Andes and southern Patagonia; 9 genera	Africa; 4 genera
Fossils:	North America, Triassic (<i>Mycetopoda</i> ?); South America, Cretaceous-paleocene (Brasil)	Pleistocene



MAP 1. Distribution of Mycetopodidae (Mutelacea) in South America.

Mycetopodidae are divided into three subfamilies:

Mycetopodinae

Edentulous shell very elongate and thin, gaping variably anteriorly. Prismatic layer narrower. Anal aperture with tendency to close above, and supra-anal not well defined. Foot extraordinarily long, cylindrical, ending in a knob, mushroom-like, protuberant. The lasidium has a long anterior filament and resembles that of *Mutela* more than those of other subfamilies.

Genera: *Mycetopoda*, *Mycetopodella*.

Anodontitinae

Shell edentulous, regular in shape. Valves not, or scarcely gaping. Periostracum marked with creases and folds. Foot regular. Supra-anal aperture distinct. Prismatic layer wide. Lasidium with very wide ribbon-like filament divergent at the distal end.

Genera: *Anodontites*, *Leila* (see appendix, p. 206).

Monocondylaeinae

Shell small, thick, solid and gaping. Hinge with one or two tuberculiform teeth. Periostracum with cloth-like sculpture. Prismatic layer wider. Supra-anal aperture and foot regular. Lasidium of an intermediate type between the other subfamilies.

Genera: *Monocondylaea*, *Fossula*, *Haasica*, *Tamsiella*.

The family name Mycetopodidae has absolute priority, dating from Gray, 1840, and it was also used by Adams and Adams (1858) and by Carpenter (1861) ("Mycetopodidae").

Anodontitinae and Monocondylaeinae were established by Modell in 1942. He restricted the subfamily Anodontitinae to the *Anodontites*, of the group *crispatus-tenebricosus-clessini*, and for the other species of the *trapesialis* groups, plus

Leila. He created Glabarinae. Since *Glabaris* according to the majority of authors is a synonym of *Anodontites* such separation should be deferred until it may be based on better grounds. Recognition of mere groups of species in the *Anodontites* complex, as proposed by Ortmann and Haas, is more acceptable. Regarding the possible use of Leilinae, see appendix.

FOSSIL MUTELACEA

Paleontological evidence in Mutelacea is very poor. A single and very doubtful specimen was referred by Ihering (1912) to the Cretaceous of southern Brasil as *Pleiodon priscus* (discussed later). Pilsbry (1921: 36) described *Mycetopoda diluculi* from Triassic beds in Pennsylvania which also contain *Diplodon*: "While the generic reference of the fossil [*M. diluculi*] is not positive, the interior being unknown, its characters, so far as they are legible, agree well with *Mycetopoda*, which appear to indicate this genus or one closely similar". Four other *Anodontites*-like species were described by Hartt (1870) and White (1887) under the generic names "*Unio*" and "*Anodonta*" for the Bahia Series of Brasil regarded as Upper Cretaceous or possibly Paleocene; these shells are smaller than the living *Anodontites*, the hinge area is unknown, and the generic identification uncertain; White suggested that some of them, *A. mawsoni* and *A. allporti*, may be *Iridina*, which is still less likely.

Frenguelli (1945) described, among other fresh-water bivalves, several species of *Paleonanodonta* and *Paleo-mutela*, from Permian-Triassic strata of Patquia, Argentina. These genera are known from the Permian of South Africa and Russia, and do not seem to be directly related with modern types of Naiades of the family Mutelidae. These may be different branches of fresh-water mussels evolved from marine ancestors which did not survive.

Viewed in their distribution in the southern hemisphere, the Mutelacea agree with that zoogeographical pattern indica-

tive of a gondwanic origin or, what Pilsbry (1911) called "Eogeic" fauna. In that "asylum", to apply the term given by Suess to his original concept of Gondwana, evolved, according to Pilsbry, several typical families of continental mollusks. However, the group from which these naiades arose is unknown; probably Mutelacea and Unionacea are not derived from a common stock but, even if they were, the groups separated at a very early time.

Ihering emphasized the importance of *Pleiodon* [= *Iridina*] *priscus* as an African element in the Brazilian Cretaceous, but the generic reference was questionable. The single fragment of the fossil valve figured by Ihering (1912), agrees more closely in umbonal and hinge characters with *Paxyodon* (type *P. ponderosus* Schumacher, 1817 = *Mya syrmatophora* Gronovius, 1891, according to clarification and subsequent designation of Olsson and Wurtz, 1951). The hinge in *Paxyodon* seems to vary with development to a pseudotaxodont condition, which appears equally in *Paxyodon ponderosus* and *Pleiodon priscus*. Furthermore, *Paxyodon* belongs to Hyriidae and its glochidium has been studied by Bonetto (1959). Thus the assumed relationship of *Pleiodon priscus* with African Mutelidae is unsound. The strata in which *P. priscus* was found probably are younger than the indicated Bauru Formation of the Upper Cretaceous.

NOTE ON THE GENUS *BARTLETTIA*

The genus *Bartlettia* Adams, 1866 (type *Etheria stefanensis* Moricand), of which *Rochanaia* Morretes, 1941, is a synonym, currently is placed within the family Etheriidae which includes: *Etheria* from Africa, *Pseudomuelleria* from India and *Acostaea* from South America.

Acostaea and *Pseudomuelleria* are monomyarians in the adult stage (only very juvenile individuals have two muscles); *Etheria* and *Bartlettia* are dimyarians. The larval form of the Ether-

iidae is still unknown. However, it is more probable that *Bartlettia* belongs to the Mutelacea²; close to, or included in the Mycetopodidae. Our personal observations as well as those made by Carcelles (1940), Pain and Woodward (1961) and Yonge (1962), indicate that the young shells of *Bartlettia* are not distorted as the adult, but very similar to (sometimes undistinguishable from) *Anodontites tenebricosus*. Adults of *A. tenebricosus* developing in crevices of rocky substratum (as shells living on the west bank of La Plata River commonly do) are strongly distorted and acquire the characteristic shape and aspect of *Bartlettia*. Also, the prismatic zone in both species is very similar and their distributions in southern South America are somewhat coincident. It is likely that *Bartlettia stefanensis*, recorded by Carcelles from the Paraguay basin, and *A. tenebricosus* belong to one and the same species. *Acostaea* is restricted to the Magdalena River in Colombia, and the fact that this species and *Pseudomuelleria* are mono-myarians is due perhaps to convergent evolution from their entirely sedentary life.

THE UNIONACEA (HYRIIDAE) OF SOUTH AMERICA AND AUSTRALIA

In 1896, Simpson related all the Australian forms of naiades to the genus *Dip-lodon*, assuming migration via Antarctica from South America. Ortmann (1912) concluded that the Australian naiades belonged to the subfamily Hyriinae, but did not establish any direct relationship among the genera. Iredale (1933/34) on the contrary emphasized the differences, creating for the Australian forms the family Propehyridellidae with four subfamilies: Velsunioninae without umbonal sculpture, Lortiellinae with ridged umbos, Cucumerunioninae with plicate umbos and large shells, and Propehyridellidae but within the Mutelidae (still including in this family the two types of embryos). They suggest

²Modell (1949) tentatively placed Etheriinae as a subfamily of Mutelidae, and Bartlettinae between Anodontitinae and Mycetopodinae.

TABLE 2. Comparison of South American and Australian Hyriidae (Unionacea)

	South America	Australia
Marsupium with interrupted network of interlaminar communications	x	x
Marsupium with continuous network	rare	?
Interlaminar connections of the non-marsupial branchiae obsolete	x	seems more developed
Central orifice on diaphragm connecting cloacal and branchial openings	rare (<i>Diplodon solidulus</i>)	x
Without orifice	x	rare
Siphonal area pigmented	(<i>D. chilensis</i>)	variable, common in <i>Hyridella</i>
Umbonal sculpture radial	x	rare, only posterior bars are radial
Umbonal sculpture with V- shaped ridges	less frequent (<i>Hyria</i> and some <i>Diplodon</i>)	common
Umbo plicate or smooth	rare	x
Schizodont hinge strong	x	rare
Hinge with small teeth	rare	common
Glochidium triangular with a S-shaped tooth in each valve ending in 1 or more spines	<i>Diplodon</i> <i>Paxyodon</i>	x
Glochidium with triangular tooth in each valve	Tribe Castalini	none
Without parasitic stage	<i>Rhipidodonta</i>	?
Heavy short shells with strong hinge	several <i>Diplodon</i>	rare

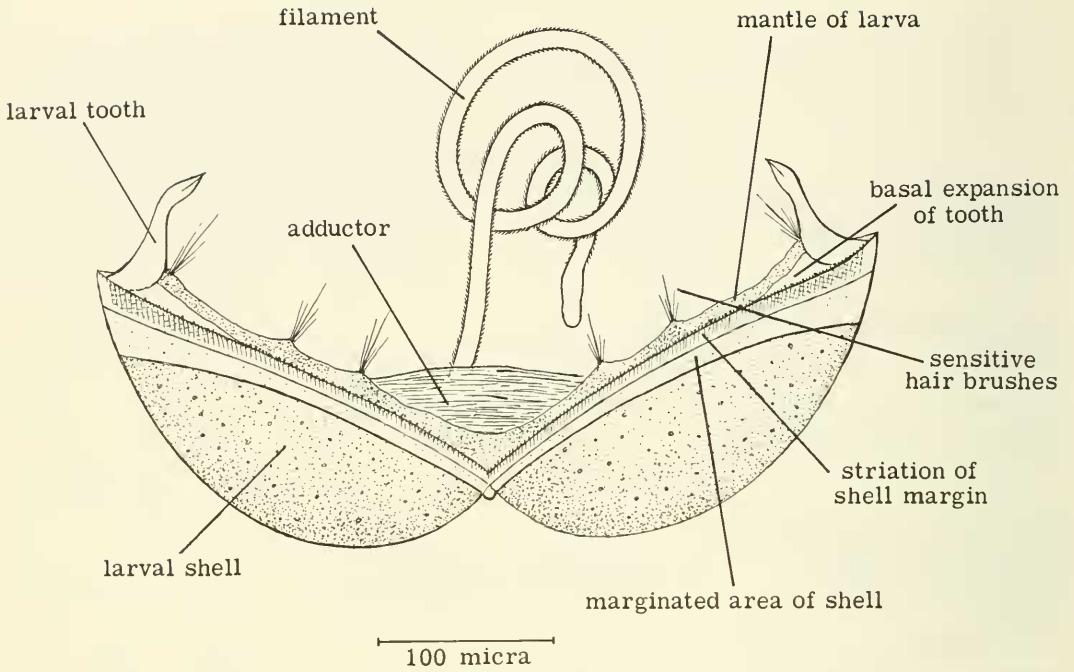


FIG. 8. Glochidium of *Velesunio ambiguus* (Philippi). Bogan River, Australia. Lateral view.

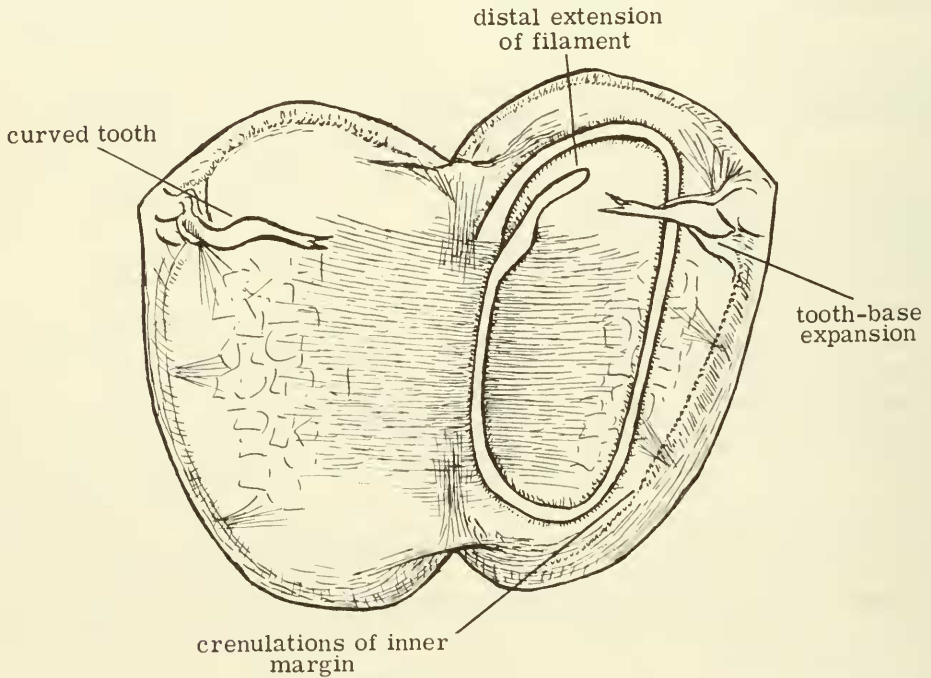


FIG. 9. Same as Figure 8. Internal view.

that the Australian naiades were derived from a basic stock of northern hemisphere ancestors which migrated to southwestern Asia in the Triassic; but a year later (1959: 243) McMichael and Iredale agreed that "an equally good case can be made for southern distribution across a temperate antarctic land mass". We understand this as referring to the Unionacea (Hyriidae) since no real Mutelacea are known from Australia.

Modell (1942, 1949), segregated many groups on the basis of the umbonal structure and hinge. In Mutelidae, which he considered the most primitive, he included Velesunioninae and Lortellinae, and he placed Cucumerunioninae in Margaritiferidae and Hyriinae and Propehyridellinae in Unionidae. Also he indicated the origin of Unionidae and Margaritiferidae as Indo-Pacific, whence the Hyridellinae invaded Australia, from where they moved to South America. This interpretation is inconsistent with the fossil evidence of Hyriidae.

Summarizing our own observations, the differences and similarities of the Unionacea (Hyriidae) in South America and Australia, are outlined in Table 2.

Classification of the Unionacea of the Southern Hemisphere is more complicated at lower taxonomic levels, especially since it seems to involve phylogenetic and zoogeographical problems. However, our data are sufficient to establish the close relationship between the forms of South America and Australia. Their affinities are closer than could be expected from divergence from common Eurasiatic ancestors, even granting an extraordinary evolutionary stability combined with a high degree of parallelism. The differences are few and it is possible to outline a lineage of *Diplodon-Hyridella*, supported by recent researches in the glochidia.

From Percival's description (1931) of the glochidium of *Diplodon lutulentus* Gould (= *Hyridella menziesi* Gray, according to McMichael and Hiscock), that of *D. menziesi hochstetteri* (Dunker) by the same authors, and the larva of *D. menziesi* from one specimen in the Carnegie

Museum collection (Fig. 16d), one can see that all these glochidia from the Australian region are entirely similar to those from South American species of *Diplodon*, in outline, shape, insertion and structure of the curved hooks.

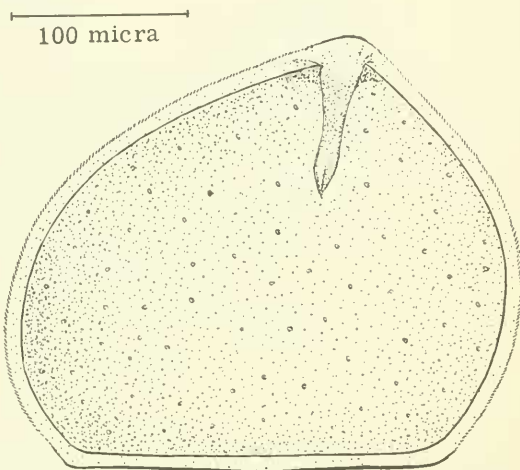


FIG. 10. Larval shell of *Velesunio ambiguus* (Philippi).

The internal organization of the glochidia of many Australian species are not well known, but according to Percival they lack the larval filament and the sensitive cirri present in the majority of *Diplodon*. Hiscock (1951) and Bonetto (1952) indicated the presence of such a filament in *Velesunio ambiguus* (Fig. 8-10).

An important variation in *Velesunio* is the basal expansion of the larval tooth over the free margin of the embryonic shell, and the presence of fine striae or crenulations along the same margin; its internal organization is, according to Bonetto, coincidental in general with *Diplodon*, although the larval filament, shorter and hollow, shows two distal expansions absent in *Diplodon*.

Except for these differences of detail, the glochidial phase in *Diplodon* and the Australian forms show greater similarity than that to be expected between *Diplodon* and other genera of South American Hyriidae, such as *Castalia*, *Castalina* and

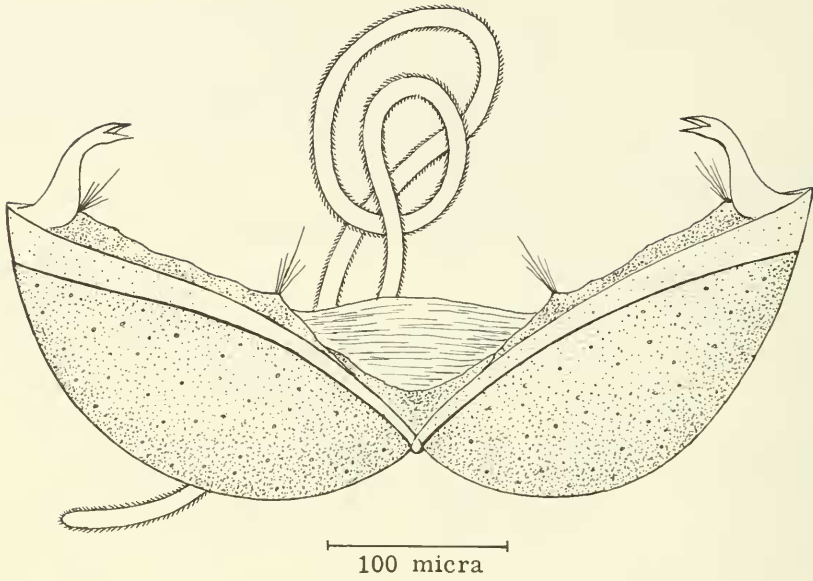


FIG. 11. Glochidium of *Diplodon delodontus delodontus* (Lamarck) Parana River, Argentina. (For nomenclature of the organs see Fig. 8).

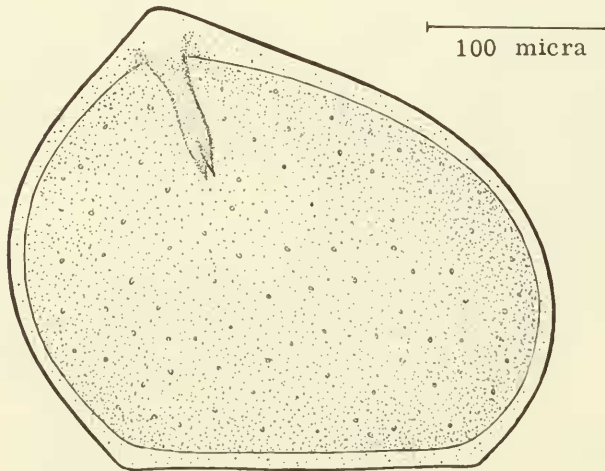
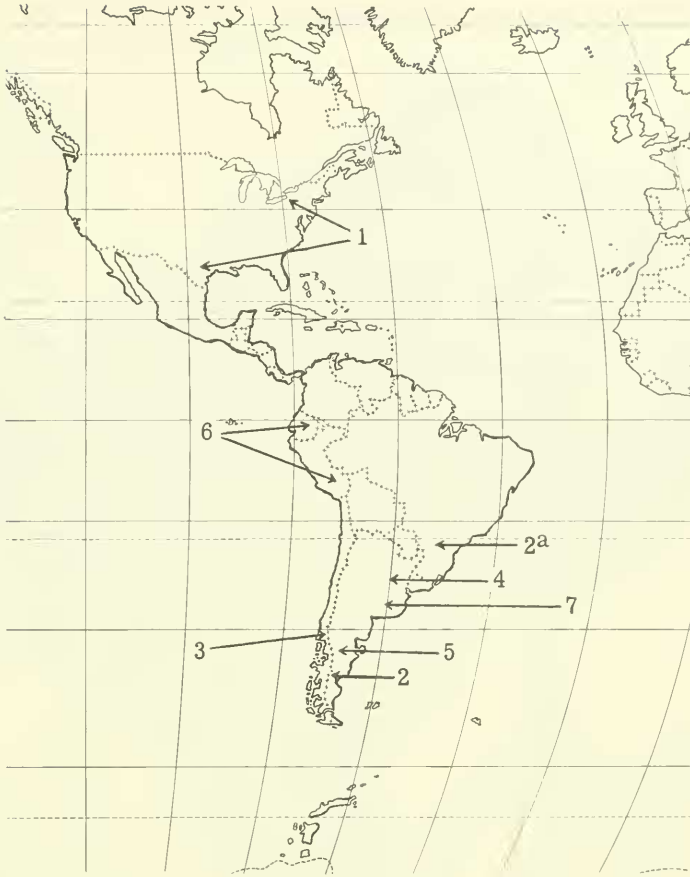


FIG. 12. Shell of the glochidium of *Diplodon delodontus delodontus* (Lamarck).



Map 2. Fossil Hyriidae. 1, Triassic Pennsylvania and Texas; 2, Paleocene southern Argentina (Patagonia); 2^a, Paleocene southern Brasil; 3, Eocene Chile; 4, Miocene NE. Argentina; 5, "Upper Tertiary" (probably Pliocene), Argentina; 6, Pliocene Peru, Ecuador; 7, Pleistocene Buenos Aires. With exception of 2 (*Paxyodon*) all other fossils belong to *Diplodon*.

Callonaia. The number of similarities in the glochidia is the basis for separation of the family Hyriidae in the southern hemisphere from all the other Unionacea.

FOSSIL HYRIIDAE

The oldest known *Diplodon* are represented by several species from the Triassic of Pennsylvania and Texas. An-

other fossil group is found in the Paleocene and Eocene of South America (southern Argentina and Chile). All these fossils are generally smaller than most of the recent species (hence comparable to the *hylaesus* group), except for Eocene Chilean forms that differ very little from the living *Diplodon patagonicus*, a form which more resembles Australian species.³

From younger and different Tertiary

³A comparative study of the types and other materials of these fossil species, is the subject of a paper now in preparation by the present authors.



MAP. 3. Distribution of Hyriidae in South America.

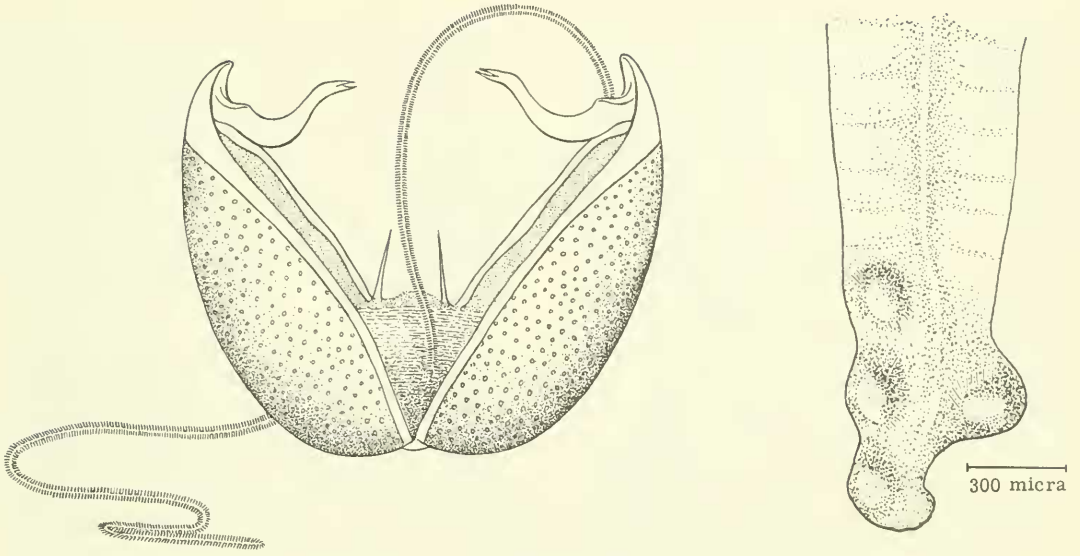


FIG. 13. Left: Glochidium of *Diplodon charruanus*, x210; right: Filament of the gill of the fish *Hoplias malabaricus* (Characidae) (common name "tararira") of the Parana River, showing the cysts produced by glochidia of *Diplodon charruanus*.

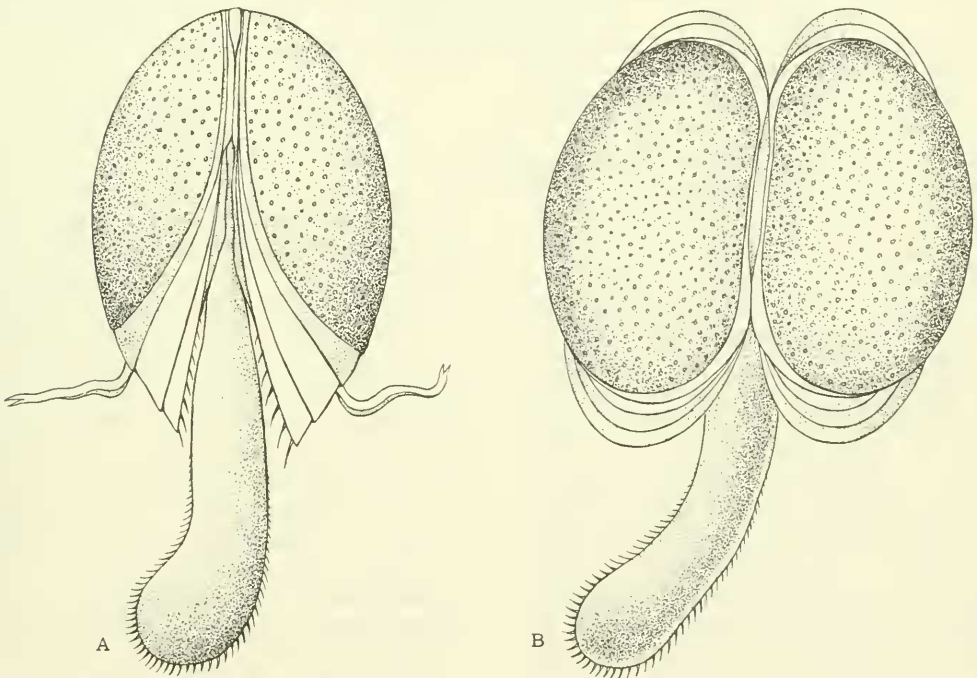


FIG. 14. A. Juvenile mussel of *Diplodon (Diplodon) charruanus* x166. B. Juvenile mussel of *Diplodon (Rhipidodonta) burroughianus (= variabilis)* showing the wide opening of the valves, x195.

levels, other fossil *Diplodon* are known from Colombia to southern Argentina, and several genera were proposed by Marshall: *Prodiplodon*, *Eodiplodon*, *Ecuadoraea*. Also Marshall's *Antediplodon* has subsequently been used for all the oldest species, despite the fact that no clear distinction between this and other named genera, or even with *Diplodon* itself, has been established. Umbonal sculpture in *Antediplodon* is of the same type as that found in living species of the *patagonicus-granosus* group, as well as in other fossils of the late Tertiary. The hinge of *Prodiplodon singewaldi* Marshall is similar to that of *D. patagonicus*. Some Triassic species such as *borealis* and *pennsylvanicus* do not seem to agree with the type species of *Antediplodon* (*Unio dumblei* Simpson). The forms from the Paleocene of Patagonia, as well as *Diplodon gardnerae* Marshall from the Pebas Formation in Peru, and the same type of *Antediplodon*, resemble the group of *hylaesus*. The division of the fossil species into genera as age-groups does not improve our taxonomic knowledge and, if a vertical classification or the maintenance of such names eventually becomes necessary, it has to be done on a more consistent basis.

Pilsbry accepted the generic identification of the fossil species under *Diplodon sensu lato*, primarily from the only conspicuous character that these fossils show: the radially sculptured umbos, not present in other living or fossil North American "Unios". This character was considered as primitive by Ihering, Marshall, Modell and Pilsbry himself. Ortman, without giving to such character enough phylogenetic significance, when diagnosing *Diplodon*, stated, however, that: "the beak sculpture is the most important feature of the group". By the presence of radial sculpture in widely separated Triassic species, Pilsbry inferred (1921: 31) that North America once possessed a large and varied Naiad fauna of South American type.

Comparison of the distribution of Tertiary and living hyriid species in South America (Maps 2 and 3) shows that the

expansion was from West to East, (earlier forms distributed along the Andes) and later especially from southwest to northeast between northern Patagonia and the rivers of the Parana system or their equivalents at the time. This type of distribution is opposite to that of the Mycetopodidae, which was from North to South in the East, without reaching the extreme southwestern areas long habited by *Diplodon*.

The rivers running across the Pampas-Chaco districts, tributaries of the Parana, are saltier than the tributaries from the East, a factor which seems to have restricted the dispersal of the Hyriidae more than that of the Mycetopodidae. Another factor may be temperature: *Diplodon* is found in some cold bodies of water in which the Mutelacea cannot live, but systematized data are yet too poor to reach conclusions.

Regarding the relationship of the recent South American and Australian Hyriidae, as indicative of an "Antarctic Way" of dispersion, fossil evidence is lacking.

THE GROUPS OF RECENT SOUTH AMERICAN HYRIIDAE

The Unionacea of South America - and of Australia for the most part - form a well defined family, Hyriidae, with shells radially sculptured at the inner laminae of the internal branchiae that are in contact with the palps, and parasitic larvae with S-shaped teeth either ending in spinulae or strongly pointed, but always without additional denticulations, and without supranal aperture; non parasitic glochidia may occur, without teeth, but in any case all the glochidia are perfectly distinguishable from those of the other families of Unionacea from the northern hemisphere. The prismatic layer is reduced to a fraction of millimeter, inconspicuous, or entirely absent.

The family name Diplodontidae Ihering 1901 (or Diplodontinae Morretes 1949) is not valid, being preoccupied by Diplodontidae Dall 1899, created for marine bivalves. Prisodontini Modell 1942 included

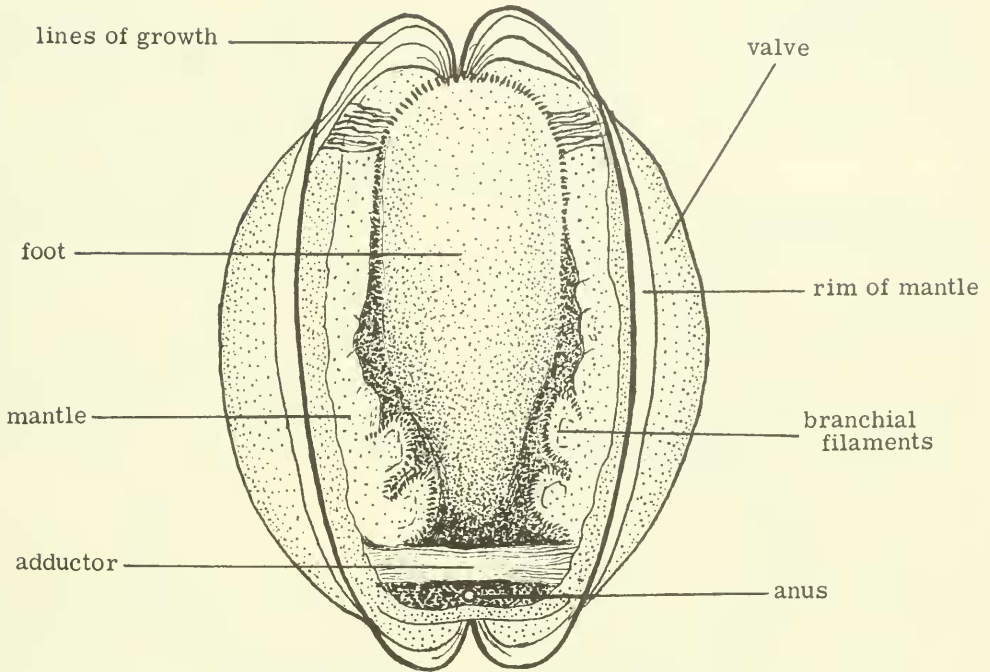


FIG. 15. Juvenile mussel of *Diplodon (Rhipidodonta) variabilis* (Maton). Ventral view.

the genus *Hyria* (= *Prisodon*) which cannot be separated as a subfamily by itself. The name Hyriidae Swainson 1840 has priority, but Diplodontini and Prisodontini can be used as tribal denominations.

The typical subfamily, Hyriinae, has the radial ribs on the umbo coalescent toward the center with very few exceptions, branchial diaphragm imperforated, anal aperture forming a simple groove without expansions, and the branchial aperture somewhat closed at the front. The glochidian tooth is triangular and not divided at the end. The glochidium is with or without larval filament, and the margin of the embryonic shells lacks crenulations.

The South American Hyriidae can be divided into the following tribes:

Tribe Diplodontini

Shell regular in shape, not alate, always with radial ribs on the umbo, but of variable growth and posterior ridge scarcely developed, except in a few more elongated and more posteriorly acute forms, as in *Diplodon parallelipipidon* (Lea) or *D. parodizi* Bonetto. Branchial opening not entirely closed at the front.

Glochidium subtriangular-scalene, with the teeth S-shaped, curved and ending in a pair of spinulae (Fig. 16, b, e); larval filament long and rolled; with 2-4 sensitive cirri. Species of direct development have no teeth or hooks in the embryonic shell, but one, or several, marked bands of growth (Figs. 11-13).

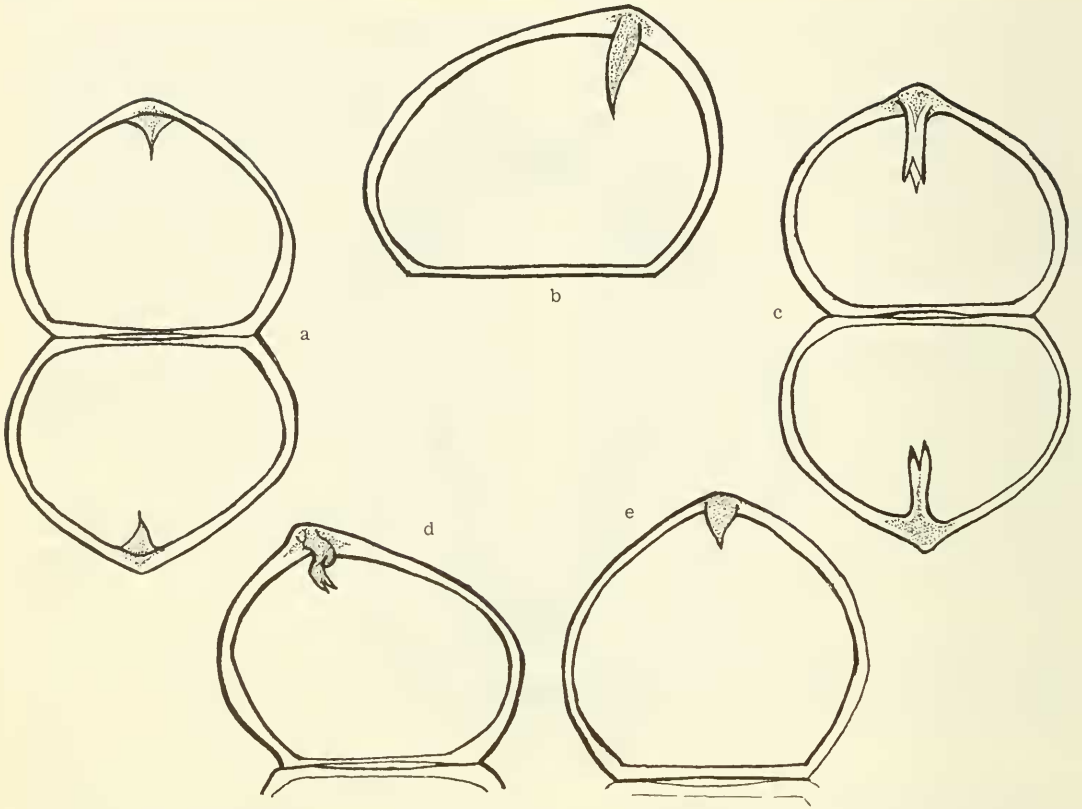


FIG. 16. Glochidia of Hyriidae. a, b, c, e, South American; d, Australian. a, *Callonaia*; b, *Diplodon solidulus*; c, *Paxyodon alatus*; d, *Hyridella menziesi*; e, *Diplodon rotundus*. All approximately x395.

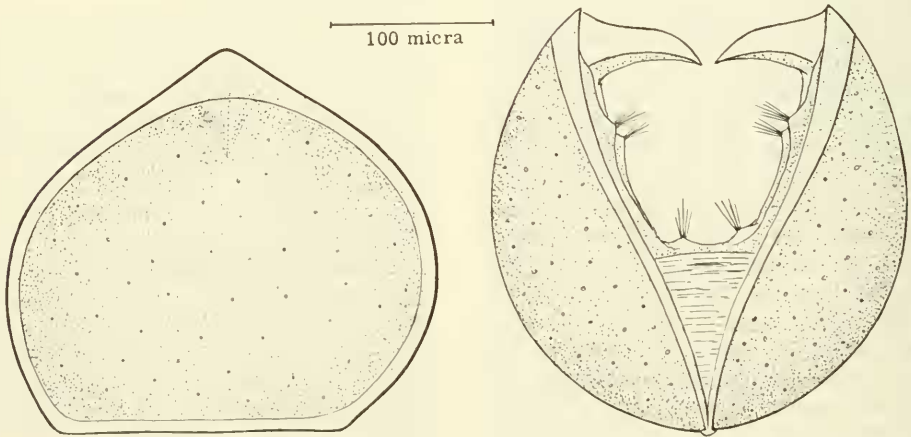


FIG. 17. Glochidium of *Castalina psammoica* (d'Orbigny) (for references see Fig. 8). Parana River at Santa Fe.

Genus *Diplodon*.

Tribe Prisodontini

Shell subrhomboidal, bi-alate or alate only behind, but always with greater posterior expansion. Umbonal sculpture radial, very strong, with conspicuous coalescence of the vertical riblets; rarely the sculpture may be inconspicuous. Posterior ridge well marked. Branchial aperture as in Diplodontini.

Glochidium triangular (isosceliform), with teeth less curved and shorter than in Diplodontini, ending in 2-3 needle-like points (the glochidium was studied in *Paxyodon alatus* (Sowerby) (Fig. 16, c) but the internal organization is not yet completely known).

Genera: *Prisodon*, *Paxyodon*.

Tribe Castaliini

Shell subquadrangular, solid, umbos elevated and umbonal cavity deep. Beak sculpture of variable development, sometimes very obsolete. Branchial opening becoming perfectly closed at the front.

Glochidium subtriangular, equilateral or isosceliform, with short, straight, triangular teeth, wide at the base but not divided at the end; cirri grouped in form of brushes; without larval filament (Fig. 16, a; 17).

Genera: *Castalia*, *Castalina*, *Castaliella*, *Callonaia*.

In the tribe Diplodontini the species present extraordinary ecological and individual variations, often repeated or mixed among the numerous local populations or demes, but without taxonomic value. Subgeneric divisions of *Diplodon* have been based on transitory shell characters only. The most reliable separation is based primarily on the parasitic or non-parasitic condition of the larvae; secondarily groups of species may be recognized by shell characters, although this sometimes presents serious difficulties on account of

the slow, intergrading, variations. *Diplodon rhuacoicus* (d'Orb.), for example, with a parasitic glochidium has been often confused from shell similarities with *D. charruanus* (d'Orb.) whose glochidium is non-parasitic; on the same account, *D. charruanus* is more closely related to the groups of *D. hylaeus* (d'Orb.) or *D. variabilis* (Maton) despite the shell differences.

Species with parasitic glochidia belong to *Diplodon sensu stricto*. In the post-larval stage the juvenile mussel shows the hooks still attached and a long, ciliated foot (Fig. 14) which soon disappears (Fig. 15). The non-parasitic species are included in the subgenus *Rhipidodonta* (type species *Diplodon variabilis* (= *paranensis*, *burroughianus*, *bulloides*), of which *Cyclomya*, *Bulloideus*, *Ecuadorea* and *Schleschiella* are synonyms. In order to avoid the mistake of placing *Rhipidodonta* as "nomen oblitum" (introduced in Article 23, section b of the International Commission of Zoological Nomenclature Code of 1961), notice must be taken that, subsequently to its establishment by Mörch in 1853, it was used by Adams and Adams, 1858, Fischer, 1887, and Thiele, 1935.

Ecuadorea Marshall 1932 was introduced for fossil forms of the very variable group of *D. hylaeus*, which is within the subgenus *Rhipidodonta*.

Schleschiella Modell, 1950 is an assemblage of unrelated species; its type, *Diplodon burroughianus* (Lea), is a synonym of *D. variabilis* (Maton), used by Mörch as type species of *Rhipidodonta*. This species has non-parasitic larvae of direct development, but Modell also included in *Schleschiella* (as a subspecies of *burroughianus*) the form *rhuacoicus*, which actually has a parasitic glochidium, as well as *D. parallelipipedon*.

Although the numerous species of *Diplodon* can be separated into minor "species-groups" for practical purposes, only the groups listed below can be diagnosed by some definite characteristics.

Key to the genus *Diplodon* (Hyriidae)

- 1a. With parasitic glochidia, *Diplodon* s.s.....2
- 1b. Glochidia non-parasitic, Subg. *Rhipidodonta*.....3
- 2a. Shell elongated, compressed laterally central costulae with marked convergence and tendency to cross, forming thick folds or nodules. External branchiae higher than the internal and marsupia placed anteriorlyGroup of *D. (D.) chilensis*
- 2b. Variable in length, diameter and altitude. Sculpture less convergent, not crossed. External branchiae of same height as the internal. Marsupia central or with posterior gravitationGroup of *D. (D.) rhuacoicus*
- 3a. Size and shape variable, generally more rounded. Sculpture less prominent and moderately convergent. Hinge teeth very variable in development.....Group of *D. (R.) variabilis*
- 3b. Small but very solid shells. Strong sculpture extended toward the middle of the shell or beyond. Several central convergent, chevron-like costulae. Hinge teeth thick and strong.Group of *D. (R.) hylaeus*

TABLE 3. COMPARATIVE SYNOPSIS OF CURRENT CLASSIFICATIONS

SIMPSON 1914	ORTMANN 1921	H A A S 1930/31	M O D E L L 1942/49
Fam. UNIONIDAE	Fam. MUTEIIDAE		Fam. HYRIIDAE
Subfam. Hyriinae (Lamphorhamphus group)	Subfam. Hyriinae		Subfam. Hyriinae ⁴
<i>Tetraplodon</i> <i>Castalina</i> <i>Castaliella</i> <i>Callonaia</i> <i>Diplodon</i> (<i>Cyclomya</i>) (<i>Bulloideus</i>) <i>Hyria</i> (<i>Triquetrana</i>) <i>Prisodon</i> (<i>Hyriana</i>)	<i>Castalia</i> <i>Castalina</i> <i>Castaliella</i> <i>Callonaia</i> <i>Diplodon</i> (<i>Cyclomya</i>) <i>Hyria</i> <i>Prisodon</i>	<i>Castalia</i> <i>Castalina</i> <i>Castaliella</i> <i>Callonaia</i> <i>Diplodon</i> (<i>Cyclomya</i>) (<i>Bulloideus</i>) <i>Hyria</i> (<i>Triquetrana</i>) <i>Prisodon</i>	} = <i>Schleschiella</i> ⁷ + <i>Bulloideus</i> + fossils: <i>Antediplodon</i> <i>Prodiplodon</i> <i>Ecuadoria</i> <i>Castalioides</i>
Fam. MUTEIIDAE	Subfam. Mutelinae		
<i>Mutela</i> <i>Monocondylaea</i>	<i>Mutela</i> <i>Monoconcyllaea</i>	<i>Monocondylaea</i> <i>Diplodontites</i> <i>Tamsiella</i> <i>Marshalliella</i> <i>Fossula</i> <i>Leila</i>	} = Monocondylaeinae ⁵
<i>Iheringiella</i> <i>Fossula</i> <i>Leila</i>	<i>Iheringiella</i> <i>Fossula</i> <i>Leila</i>		
<i>Anodontites</i> (<i>Virgula</i>) (<i>Steganodon</i>) <i>Mycetopoda</i>	<i>Anodontites</i> (<i>Lamphroscapha</i>) <i>Mycetopoda</i>	<i>Anodontites</i> (<i>Lamphroscapha</i>) <i>Mycetopoda</i>	Subfam. Glabariinae ⁵ + <i>Glabaris</i> Subfam. Anodontitinae ⁵
			Subfam. Mycetopodidae ⁵ + <i>Mycetopodella</i>

⁴With glochidium larva.
⁵With *Lasidium* larva.
⁶*Lasidium*-like.
⁷See page 201.

TABLE 4. SYNOPSIS OF PRESENT CLASSIFICATION

MUTELACEA	{	MUTELIDAE		Africa		
		MYCETOPODIDAE	{	ANODONTITINAE MYCETOPODINAE MONOCONDYLAEINAE LEILINAE ⁸	} South America	
UNIONACEA	{	HYRIDAE	{	HYRINAE		{ <i>Prisodontini</i> <i>Castaliini</i> <i>Diplodontini</i>
				VELESUNIONINAE, etc. HYRIDELLINAE, etc.		
		UNIONIDAE	{	LAMPSILINAE ANODONTINAE UNIONINAE	} North America, Eurasia, Africa	
		MARGARITEFERIDAE				

⁸See Appendix, page 206.

PRESENT CLASSIFICATION OF SOUTH AMERICAN NAIADES
AND RELATED AFRICAN FORMS

Superfamily UNIONACEA

Families UNIONIDAE Fleming 1828 (with several subfamilies in the northern hemisphere) and MARGARITIFERIDAE Haas 1940⁹ (Margaritanidae Ortmann 1910) are not included in the Neotropical region (see Table 4).

Family HYRIIDAE Swainson (Hyria-nae) 1840; Herrmannsen 1847

= Hyridinidae Carpenter 1861; Diplodontidae Ihering 1901 non Dall 1899; Hyriinae Ortmann 1911.

Type genus: *Prisodon* Schumacher 1817. = *Hyria* Lamarck 1819 non Stephens 1829, Robineau 1863, Insecta; *Hyria* Gronovius 1763 -Meuschen 1778 *nomen nudum*; *Hyria* Blainville 1821.

Subfamily HYRIINAE Swainson 1840 (restricted South America) = Hyria-dae Agassiz 1847; Prisodontinae Modell 1942, Morretes 1949.

Tribe Prisodontini

Genus *Prisodon* Schumacher 1817. = *Naia* Swainson 1840; *Harmandia* Rochebrune 1881.

Type: by subsequent designation of Olsson and Wurtz 1951: *P. obliquus* Schumacher.

Subgenus *Triplodon* Spix 1827

Type: *T. rugosum* Spix (= *Hyria corrugata* Lamarck).

Subgenus *Triquetrana* ? Simpson 1900.

Type: *Unio stevensi* Lea.

Genus *Paxyodon* Schumacher 1817.

Type: *P. ponderosus* Schumacher = *Mya syrmatophora* Gronovius 1781.

Tribe Castaliini

Genus *Castalia* Lamarck 1819. = *Tetraplodon* Spix 1827.

Type: *Castalia ambigua* Lamarck non Sowerby = *inflata* d'Orb. ?

Genus *Castalina* Ihering 1891.

Type: *C. martensi* Ihering.

⁹The "Official List of Family-Group Names" [of the International Commission on Zoological Nomenclature] London 1958, p. 57, establishes: "Margaritiferidae Haas 1940, Field Mus. Publ. (Zool) 24: 119, as validated under the Plenary Powers (type genus: *Margaritifera* Schumacher 1816)" [emend. of *Margartifera*]. The name Margaritiferidae was used previously by Henderson 1929; in 1936, however, Henderson used Margaritiferinae as a subfamily of Unionidae.

Genus *Callonaia* Simpson 1900.

Type: *C. duprei* Simpson.

Genus *Castaliella* Simpson 1900.

Type: *C. sulcata* (Recluz)

Tribe Diplodontini

Genus *Diplodon* Spix 1827. = *Iridea* Swainson 1840.

Type: *Diplodon ellipticum* Spix.

Subgenus *Rhipidodonta* Mörch 1853. = *Cyclomya* Simpson 1900. *Bulloideus* Simpson 1900. *Ecuadoreia* Marshall 1932. *Schleschiella* Modell 1950.

Type: *Unio variabilis* Maton = *paranensis* + *burroughianus* Lea.

Genus *Diplodontites*¹⁰ Marshall 1922.

Type: *D. cookei* Marshall

Australian subfamilies HYRIDELLINAE and VELESUNIONINAE are known to have a glochidium larva; in Lortuellinae, Cucumerunioninae and Rectidentidae the larva is unknown.

Superfamily MUTELACEA

Family MUTELIDAE Gray 1847 (restricted to Africa).

= Muteladae Conrad 1853; "Platiris I" group Lea; Iridinidae Bourguignat 1886; Pliodontidae Rochebrune.

Type genus: *Mutela* Scopoli 1777. = *Spatha* Lea 1838; *Calliscapha* Swainson 1840; *Mutelina* Bourguignat 1855; *Pseudomutela* Simpson 1900.

Family MYCETOPODIDAE Gray 1840 (restricted *sensu* Conrad 1853).

= Mycetopidae Carpenter 1861.

Type genus: *Mycetopoda* d'Orbigny 1835.

Subfamily MYCETOPODINAE Adams and Adams 1858 (Mycetop-inae).

Genus *Mycetopoda* d'Orbigny 1835 (*Mycetopus* 1847).

Type: *M. siliquosa* (Spix).

Genus (?) *Mycetopodella* Marshall 1927.

Type: *M. falcata* (Higgins).

¹⁰The inclusion of this very little known genus, *Diplodontites*, within the Hyriinae is only tentative. It has a prismatic layer like a mutelid, and other characters approach *Diplodon*, but its embryology is unknown.

Subfamily MONOCONDYLAEINAE Modell 1942. = Monocondylae-idae Morretes 1949.

Type genus: *Monocondylaea* d'Orbigny 1835. = *Aplodon* Spix (non Rafinesque 1818). *Spixioconcha* Pilsbry 1893.

Type: *M. paraguayana* d'Orbigny.

Genus *Haasica* Strans 1932. = *Marshalliella* Haas 1931 (non Kieffer 1913, nec Poppius 1914). *Iheringiella* Pilsbry 1893. *Plagiodon* Lea 1856.

Type: *Plagiodon balzani* Ihering.

Genus *Fossula* Lea 1870

Type: *Monocondylaea fossiculifera* d'Orbigny.

Genus *Tamsiella* Haas 1931

Type: *Monocondylaea tamsiana* Dunker.

Subfamily ANODONTITINAE Modell 1942. = Glabariinae Modell 1942.

Type genus: *Anodontites* Bruguière 1792. = *Patularia* Swainson 1840; *Glabaris* Gray 1847; *Styganodon* Martens 1900; *Ruganodontites* Marshall 1931; *Pachyanodon* Martens 1900.

Type: *A. crispata* Bruguière¹¹.

Subgenus *Lamphroscapha* Swainson 1840. = *Virgula* Simpson 1900.

Type: *A. ensiformis* (Spix).

? Subfamily LEILINAE Morretes 1949 (See Appendix below).

Type genus *Leila* Gray 1840. = *Columba* Lea 1833 (non Linnaeus 1758).

Type: *Anodonta blainvilleana* Lea.

APPENDIX

New observations made on *Leila blainvilleans* (Lea) revealed a clearer distinction from *Anodontites*. *Leila* has a pair of well developed contractile siphons formed by a separate fold of the mantle and not by fusion of the mantle edges, and consequently a well marked pallial sinus. The palps are low and elongated instead of high and rounded as in *Anodontites*. The shell is more winged and gaping, with a

series of 6 or 7 parallel dorsal scars which are not present in other Mycetopodidae, but represented in *Mutela* by a single one. The prismatic layer is practically absent.

The lasidium of *Leila* is of a type closer to the larva of *Mutela*, of large size (three times larger than in *Anodontites*), with a long filament instead of a ribbon-like organ of attachment, the ciliated lobes well separated and without cirri at the posterior end.

All these characters seem to indicate

¹¹To this group, apparently, belongs *Bartlettia stefanensis* (Moricand). If, however, the previously supposed differences are sustained by further research on the *Bartlettia-Acostaea* group, then the name Bartlettinae Modell 1942 should have priority. (See note on page 190).

that the differences between *Anodontites* and *Leila* are of an importance greater than previously assumed. Modell (1942-49) included *Leila* with his *Glabariinae* (= *Anodontitinae* in our scheme), but the genus constitutes rather a subfamily by itself, for which we have the name *Leilinae* Morretes 1949; that author, however did not indicate the reasons for the separation.

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ZUSAMMENFASSUNG

TAXONOMIE UND ZOOGEOGRAPHISCHE BEZIEHUNGEN DER SÜDAMERIKANISCHEN NAIADEN (PELECYPODA: UNIONACEA UND MUTELACEA)

Für die südamerikanischen perlmutterigen Süßwassermuscheln, welche früher alle in die Superfamilie Unionacea eingereiht wurden, wird hier eine natürliche Klassifikation vorgeschlagen. Die seit dem Ende des vorigen Jahrhunderts gebräuchlichen Systeme, die nach hauptsächlich konchyliologischen und nur teilweise anatomischen Richtlinien aufgestellt wurden, werden hier in Hinblick auf neuere embryologische und phylogenetische Forschungen besprochen, insbesondere was die Struktur und Entwicklung der verschiedenen Larventypen anbelangt. Untersuchungen der Autoren innerhalb der letzten 10 Jahre haben die Existenz einer "Lasidium"-Larve bestätigt, die seit ihrer erstmaligen Entdeckung durch Ihering im Jahre 1891 nie mehr beobachtet worden ist. Diese Larve ist für die südamerikanischen Gattungen *Anodontites Mycetopoda*, *Monocondylaea* und *Leila* typisch. Gleichzeitig haben die Untersuchungen anderer Forscher an afrikanischen Arten von *Mutela* gezeigt, dass diese eine Larve haben, die, wenn sie auch nicht mit dem Lasidium identisch ist, ihm doch in den wesentlichen Strukturen sehr gleicht. Ein vergleichendes Studium des Aufbaus und der Entwicklung dieser Larven zeigt einen Rangunterschied von Familiengrad zwischen den Muteliden Afrikas und den Mycetopodiden Südamerikas an. Die nahe Verwandtschaft dieser beiden Familien und ihre aussergewöhnlich auffällige Divergenz gegenüber denjenigen Süßwassermuscheln, die durch die wohlbekannte "Glochidium"-Larve gekennzeichnet sind, ermöglichen andererseits die Aufstellung einer neuen Superfamilie MUTELACEA. Alle übrigen Süßwassermuscheln mit Glochidien verbleiben in den UNIONACEA.

Die Mutelacea leben heute in der südlichen Hemisphäre, mit Ausnahme von Australasien. Es ist unbekannt ob die südamerikanischen von den afrikanischen Formen abgeleitet sind oder umgekehrt. Die anatomischen und embryologischen Unterschiede zwischen den Mutelidae und den fortgeschritteneren Mycetopodidae scheinen auf eine frühe Trennung hinzudeuten. Paläontologische Aufzeichnungen fehlen beinahe völlig. In Nordamerika bezeichnete Pilsbry Fossilien aus den Triasformationen Pennsylvaniens als *Mycetopoda*-ähnliche Muscheln; "*Pleiodon priscus*", von Ihering aus der Kreide Brasiliens beschrieben, ist nicht, wie angenommen, ein Mutelide, sondern ein Hyriide der Gattung *Pexyodon*. Verschiedene Angaben über *Anodontites*-ähnliche Fossilien aus der Kreide Bahias in Brasilien sind äusserst zweifelhaft.

Wir teilen die südamerikanischen Mutelacea, d.h. die Mycetopodidae, in 3 Unterfamilien ein: die Mycetopodinae, Anodontinae und Monocondylinae; eine weitere Unterfamilie, die Leilinae, kann man vielleicht ebenfalls auf Grund neuerer embryologischer und anatomischer Erkenntnisse unterscheiden. Andere, in früheren Klassifikationen aufgestellte Gruppen mit Rangstufe einer Unterfamilie lassen sich nicht aufrechterhalten, da ihre Kennzeichen nicht genügend beständig und die Zwischenstufungen zahlreich sind.

Die südamerikanischen Unionacea gehören der Familie Hyriidae an, welche auch in Australien vorkommt, aber auf der übrigen Welt fehlt. Die ausschliesslich südamerikanischen Formen gehören der Unterfamilie Hyriinae an und werden in 3 Tribi eingeteilt: Diplodontini, Castaliini und Prisodontini. Insbesondere die Diplodontini, deren zahlreichste Vertreter der Gattung *Diplodon* angehören, sind näher mit den Formen Australiens und Neuseelands verwandt. Auch hier blieben Versuche die Gattung in eine Anzahl von Untergattungen zu zergliedern, infolge der Schwierigkeit beständige Merkmale zu definieren, erfolglos. Vom embryologischen Standpunkt aus kann man aber 2 Einheiten von subgenerischem Wert unterscheiden: *Diplodon s.s.*, mit parasitischen Glochidien und *Rhipidodonta* mit nicht parasitischen Glochidien, d.h. solchen mit direkter Entwicklung. Es gibt paläontologische Angaben über das Vorkommen von Hyriiden im nordamerikanischen Trias, im südamerikanischen Paläozän und im Eozän von Chile, wobei die letzteren Fossilien den heute in dieser Gegend lebenden Arten, wie auch verwandten australischen Arten, sehr ähneln. Alle diese Fossilien gehören zu der Gattung *Diplodon*, von welcher auch verschiedene andere Arten in jüngeren Schichten aus dem mittleren und oberen Tertiär des südamerikanischen Kontinentes vorkommen.

Die den sogenannten "Süsswasseraustern" angehörige monotypische Gattung *Bartlettia*, die man allgemeinerweise zu den Etheriiden rechnet, gehört wahrscheinlich einer polymorphen Art der Mutelacea, *Anodontites tenebricosus* an. Die larvären Stadien der Etheriiden sind noch unbekannt. Höchstwahrscheinlich aber dürften weitere Untersuchungen ergeben dass diese Familie, falls sie überhaupt als solche erhalten bleibt, unter die Mutelacea einzureihen sein wird.

Tabellen werden hier gegeben, welche die verschiedenen seit 1900 gebräuchlichen Klassifikationssysteme vergleichen und auch das hier angewandte System von den Superfamilien bis zu den Untergattungen zeigen.

RÉSUMÉ

TAXONOMIE ET RELATIONS ZOOGEOGRAPHIQUES DES NAIADES DE L'AMÉRIQUE DU SUD (PELECYPODES: UNIONACEA ET MUTELEACEA)

Un système naturel de classification est proposé pour les moules nacrées fluviatiles qui étaient jusqu'à présent toutes rangées dans la superfamille Unionacea. Les systèmes en usage depuis la fin du siècle dernier, basés principalement sur des caractères conchyliologiques et partiellement sur des caractères anatomiques, sont ici discutés à la lumière de recherches embryologiques et phylogénétiques récentes, spécialement en ce qui concerne la structure et le développement des différents types larvaires.

Les recherches faites par les auteurs pendant les 10 dernières années ont confirmé l'existence d'une larve, le "lasidium", qui n'avait plus été observé depuis sa découverte première par Ihering en 1891. Cette larve est typique pour les genres sudaméricains *Anodontites*, *Mycetopoda*, *Monocondylaea* et *Leila*. Simultanément, des recherches faites par d'autres auteurs sur certaines espèces de *Mutela* de l'Afrique y ont révélé l'existence d'un type larvaire qui, s'il n'est pas exactement conforme au lasidium, en a néanmoins les traits structuraux essentiels. Des études comparatives sur l'organisation

et le développement de ces larves permettent de formuler les différences entre les mutélidés de l'Afrique et les mycétopodidés de l'Amérique du Sud. D'autre part, les grandes affinités entre ces 2 familles ainsi que leur extraordinaire divergence embryologique d'avec toutes les moules fluviatiles caractérisées par les larves si bien connues du type "glochidium", permettent leur groupement dans une nouvelle superfamille, les MUTELACEA. Toutes les autres moules sudaméricaines à glochidies restent dans les UNIONACEA.

Les Mutelacea vivent exclusivement dans l'hémisphère austral, sauf en Australasie. Nous ne sommes pas en mesure de juger si les groupes américains dérivent des groupes africains, ou vice versa. Les différences anatomiques et embryologiques entre les Mutelidae et les Mycetopodidae, plus évolués, paraissent indiquer une séparation ancienne. Nous ne disposons que d'indices paléontologiques fort restreints: ils font défaut pour l'Australie et l'Afrique; en Amérique du Nord Pilsbry attribue certains fossiles du triassique de Pennsylvanie à un genre ressemblant à *Mycetopoda* tandis que le "*Pliodon priscus*", décrit par Ihering du crétacé brésilien, n'est pas un Mutélidé comme on le croyait, mais un Hyriidé du genre *Paxyodon*. Enfin, certaines références à des fossiles du type de *Anodontites*, du Crétacé de Bahia au Brésil, sont fort douteuses.

Les Mutelacea de l'Amérique du Sud, les Mycetopodidae, sont divisés en 3 sous-familles: les Mycetopodinae, Anodontinae et Monocondylaeinae. Une sous-famille additionnelle, les Leilinae sera peut-être à introduire suivant les recherches récentes, mais il n'est pas possible de maintenir d'autres groupes, indiqués dans les classifications antérieures, au rang de sous-familles, car leurs distinctions anatomiques et conchyliologiques sont insuffisamment tranchées.

Les Unionacea de l'Amérique du Sud appartiennent à la famille des Hyriidae, qui vit aussi en Australie, mais est absente du reste du monde. Les formes exclusivement sudaméricaines sont rangées dans la sous-famille Hyriinae et divisées en 3 tribus: les Diplodontini, Castaliini et Prosodontini. Les Diplodontini en particulier, dont le groupe le plus nombreux est formé par le genre *Diplodon*, sont les plus étroitement alliés aux formes australiennes et néozélandaises. Tous les essais de distinguer divers sous-genres ont échoué en raison de l'impossibilité d'en définir des caractères constants, même approximativement.

Du point de vue embryologique, pourtant, nous pouvons distinguer 2 groupes de valeur sous-générique: *Diplodon s.s.*, à glochidies parasites et *Rhipidodonta* à glochidies non-parasites, c'est à dire à développement direct. Nous disposons de renseignements paléontologiques sur les hyriidés: des fossiles ont été décrits du triassique de l'Amérique du Nord, du paléocène de l'Argentine australe et de l'éocène du Chili, ces derniers étant très proches des espèces qui vivent actuellement dans la région, ainsi que des groupes apparentés de l'Australie. Tous ces fossiles appartiennent au genre *Diplodon*, dont on connaît nombre d'autres espèces de différentes couches plus récentes des niveaux tertiaires moyens et supérieurs distribués de par le continent sudaméricain.

Le genre monotypique *Bartlettia*, connu sous le nom de "huitres d'eau douce" et couramment inclus dans les Etheridae, fait très probablement partie d'une espèce polymorphe de Mutelacea, l'*Anodontites tenebricosus*. Les stades larvaires des Ethéridés ne sont pas encore connus mais nous pensons que les recherches futures montreront peut-être que cette famille, si elle est maintenue, se rangera parmi les Mutelacea.

Des tableaux comparant les différents systèmes de classification en usage depuis 1900 sont ici donnés, ainsi que celui ici adopté, allant du niveau de la superfamille à celui du sous-genre.

RESUMEN

TAXONOMIA Y RELACIONES DE LAS NAIADES DE SUDAMERICA

El presente trabajo propone una clasificación natural de las almejas nacaríferas de agua dulce sudamericanas que se agrupaban en la superfamilia Unionacea. Los sistemas conocidos desde fines del siglo pasado, basados principalmente en caracteres conchológicos y en parte anatómicos, se discuten a la luz de recientes investigaciones embriológicas y filogenéticas, especialmente acerca de la estructura y desarrollo de los diferentes tipos de larva que hasta ahora eran muy poco conocidos.

Investigaciones llevadas a cabo por los autores en los últimos diez años han confirmado la existencia de la larva "lasidio", que no había sido observada de nuevo desde

su descubrimiento por Ihering en 1891; esta larva es típica de los géneros sudamericanos *Anodontites*, *Mycetopoda*, *Monocondylaea*, *Leila* y afines. Al mismo tiempo, otros estudios realizados en especies africanas de *Mutela* han revelado la existencia de un tipo de larva que, si bien no es exactamente igual al lasidio, participa del mismo plan de estructura. El estudio comparativo de la organización y desarrollo de estas larvas permite la diferenciación de dos familias, Mutelidae y Mycetopodidae, en África y Sudamérica respectivamente. Además, la estrecha relación entre esas dos familias y el extraordinario contraste de su embriología frente a las otras almejas cuyo tipo de larva es el bien conocido gloquidio, permiten agruparlas y distinguirlas en una nueva superfamilia MUTELACEA, mientras que los restantes géneros y familias se conservan en la superfamilia UNIONACEA.

Las Mutelacea actuales son exclusivas del hemisferio sur pero ausentes en Australasia. Un posible origen africano de los grupos sudamericanos, o viceversa, no ha sido demostrado todavía. Las diferencias embriológicas y anatómicas entre las Mutelidae y las más avanzadas Mycetopodidae parecen indicar una separación remota. Las referencias a hallazgos fósiles de Mutelacea son raras y carecen de confirmación: ninguna en África o Australasia; en Norte América se encontraron moldes, atribuidos por Pilsbry a *Mycetopoda* o un género similar, en el Triásico de Pennsylvania; "*Pleiodon priscus*" descrito por Ihering del Cretáceo del Brasil, no es un mutélido como se había creído sino que pertenece al género *Paxyodon* de los Hyriidae. Otras referencias sobre almejas de tipo *Anodontites* del Cretáceo de Bahía, Brasil, son también muy dudosas.

Las Mutelacea sudamericanas, Mycetopodidae, se dividen en tres subfamilias fácilmente reconocibles: Mycetopodinae, Anodontitinae y Monocondylaeinae; otra subfamilia, Leilinae, podría aceptarse basada en estudios más recientes. Otros grupos al nivel de subfamilia intentados por previas clasificaciones no pueden mantenerse, por insuficiente caracterización y demasiada intergradación.

Las Unionacea sudamericanas pertenecen a la familia Hyriidae, viviente también en Australasia pero ausente en otras partes del mundo. Aquellas que son exclusivamente sudamericanas forman la subfamilia Hyriinae, dividida en tres tribus: Diplodontini, Castaliini y Prisdontini; las Diplodontini, especialmente, están más relacionadas con las formas de Australia y Nueva Zelanda; el grupo más numeroso es el género *Diplodon*, y, también aquí, previos intentos para distinguir subgéneros han fallado por la dificultad en definir caracteres constantes. Desde el punto de vista embriológico, sin embargo, se pueden distinguir dos grupos de valor subgenérico: *Diplodon s.s.*, con gloquidias parásitas, y *Rhipidonta*, con gloquidias no parásitas, es decir con desarrollo directo.

Fósiles de Hyriidae, todos pertenecientes al género *Diplodon*, han sido encontrados en el Triásico de Norte América, (Pennsylvania y Texas), Paleoceno de Argentina austral y Eoceno de Chile, estos últimos ya muy parecidos a las especies actuales de la región así como a grupos actuales afines de Australia. Se conocen también otros fósiles del mismo género de otros niveles terciarios en diferentes localidades sudamericanas.

El género monotípico *Bartlettia*, de las llamadas "ostras de agua dulce", corriente-mente incluido en la familia Etheriidae, muy probablemente pertenece a una especie polimorfa de Mutelacea, *Anodontites tenebricosus*. Estadios larvales de estos y otros Etheriidae son desconocidos, pero futuras investigaciones pueden comprobar que las Etheriidae, si deben mantenerse como tales, pertenecen a las Mutelacea.

Se dan tablas comparativas de los diferentes sistemas de clasificación propuestos desde 1900, así como se presenta el sistema ahora propuesto, desde el nivel de superfamilia hasta subgénero.

АБСТРАКТ

ТАКСОНОМИЯ И ЗООГЕОГРАФИЧЕСКОЕ РОДСТВО ЮЖНОАМЕРИКАНСКИХ НАЯД

Дж. Дж. Пародиз и А. А. Бонетто

Естественная система классификации предлагается для южноамериканских пресноводных жемчужниц, которые раньше были сгруппированы в сверхсемейство *Unionacea*. Системы, принятые в конце прошлого столетия, которые были базированы главным образом на конхиологических и только отчасти на анатомических характерах, обсуждаются в связи с недавними эмбриологическими и филогенетическими исследованиями, в особенности же в связи со структурой и разви-

тием различных типов личинок. Исследования, произведенные за последние 20 лет, подтвердили существование личинки "ласидиум", найденной Ирингом в 1891 г., но не наблюдавшейся с тех пор другими авторами. Эта личинка типична для южноамериканских родов *Anodontites*, *Mycetopoda*, *Monocondylaea* и *Leila*. В то же время исследования других работников африканских видов рода *Mutela* нашли личинку не совсем сходную с ласидиумом, но структурно близкую к нему в главных чертах. Сравнительное изучение этих структур и их развития показало семейственное сходство между *Mutelidae* Африки и *Mycetopodidae* Южной Америки. С другой стороны, близкое родство между этими двумя семействами и их чрезвычайно различное эмбриологическое развитие по сравнению с другими пресноводными жемчужницами, для которых так характерна личинка "глохидиум", диктуют их выделение в новое сверхсемейство **MUTELACEA**. Все другие южноамериканские пресноводные жемчужницы с личинкой типа глохидиум остаются в **UNIONACEA**.

Виды сверхсемейства **Mutelacea** сегодня живут в южном полушарии, за исключением Австралии. Неизвестно, произошли ли южноамериканские группы от африканских, или наоборот. Анатомические и эмбриологические различия между *Mutelidae* и более развитым семейством *Mycetopodinae*, повидимому, указывают на их древнее разделение. Палеонтологические данные редки: и таковых не существует для Африки или Австралии; в Северной Америке отпечатки из триасовых пластов штата Пеннсилвания были отнесены Генрихом Пилсбри к жемчужницам *Mycetopoda*; *Pleiodon priscus*, описанный Ирингом из меловых пластов Бразилии, не является мутелидом, как это предполагали, но принадлежит к роду *Paxiodon* (*Hyriidae*). Некоторые ссылки на ископаемые из меловых пластов в Бразилии, в Бразилии, раковины вроде *Anodontites* очень сомнительны.

Южноамериканские **Mutelacea**, т.-е. *Mycetopodidae* разделяются на три подсемейства: *Mycetopodidae*, *Anodontitinae* и *Monocondylaeinae*; другое подсемейство *Leiliinae* может быть принято в эту группу, судя по результатам недавних исследований его анатомии и эмбриологии. Другие группы на уровне подсемейства, указанные в предыдущих классификациях, не могут быть удержаны из-за недостаточности их характеров и множества интерградаций.

Южноамериканские **Unionacea** принадлежат к семейству *Hyriidae*, которое находится также и в Австралии, но отсутствует в остальном мире; исключительно южноамериканские формы, принадлежащие к подсемейству *Hyriinae*, разделяются на три трибы: *Diplodontini*, *Castaliini* и *Prisodontini*. Подсемейство *Diplodontini* состоящее, главным образом из рода *Diplodon*, особенно близко родственно австралийским и новозеландским формам. Тут снова попытка разделения его на подроды неудается, по причине трудности установить постоянство характерных черт. С точки зрения эмбриологии, мы можем различить два особых признака подродового значения: *Diplodon ss.*, с паразитарной глохидией, и *Rhipidontia*, с глохидией непаразитарной; другими словами, с прямым развитием. Есть палеонтологические данные о семействе *Hyriidae* в триасе Северной Америки, в палеоцене Южной Аргентины и в эоцене Чили, ископаемые которого очень близки к видам ныне живущим в Чили, а также и к родственным группам в Австралии. Все эти ископаемые принадлежат к роду *Diplodon*, другие виды которого из пластов в различных плоскостях среднего и верхнего триаса, рассеяны по континенту Южной Америки.

Монотипный род *Bartlettia*, так называемых "пресноводных устриц", теперь отнесен к семейству *Etheriidae* и очень возможно принадлежит к полиморфному виду *Anodontites tenebricosus* сверхсемейства **Mutelacea**.

Сравнительные таблицы тут даны для разных систем классификации, начиная с 1900 года и кончая системой принятой нами, со сверхсемейства и до подродового уровня.

